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NEW SPECIES OF FOSSIL VAMPIRE BATS (MAMMALIA: CHIROPTERA: DESMODONTIDAE) FROM FLORIDA AND VENEZUELA

Gary S. Morgan, Omar J. Linares, and Clayton E. Ray

Abstract.—A new species of vampire bat is described from a partial skull and several postcranial elements from the early Pleistocene of Florida. Similar in size to the living *Desmodus rotundus*, it is considerably smaller than the only previously recognized species of North American fossil vampire, *D. stocki*. Characters that distinguish the new species include the large mastoid process, narrow occiput, reduced ventral flexion and posterior inflation of the braincase, and posteriorly directed foramen magnum. It occurs in fossil deposits ranging in age from approximately 1.8 to 1.0 million years (early to middle Irvingtonian), and is more than one million years older than any previously known vampire bat.

A second new species of giant vampire bat is described from two partial skeletons recovered from surficial deposits of uncertain Late Quaternary age in Cueva del Guácharo, Monagas, Venezuela. This new species is larger than any other described vampire and differs as well in its relatively slender and delicate skull, and mandible with straight ventral border and pockets behind incisors almost lacking. Skeletal fragments from caves in West Virginia and Yucatán represent vampires of similarly large size but undetermined affinities.

Fossil remains, undoubtedly in part at least of Recent age, of the common vampire, Desmodus rotundus, were recognized by Lund from caves near Lagoa Santa, Minas Gerais, Brazil, in the course of his explorations of 1835-1844 (Ray et al. 1988). Remains thought to be Recent in age have been assigned to Desmodus rotundus from three caves, and to Diphylla ecaudata from one cave, in Venezuela (Linares 1968, 1970). The new species described here is the first evidence of an extinct vampire in South America. Fossil vampires were first reported from North America in a footnote to a paper on a new species of Pleistocene terrestrial gastropod from a cinnabar mine near Terlingua, Texas (Cockerell 1930). This large extinct vampire bat was later described as Desmodus stocki (Jones, 1958) from deposits of late Pleistocene (Rancholabrean) age in San Josecito Cave, Nuevo Leon, northern

Mexico. Gut (1959) described a second species, D. magnus, from the late Pleistocene Reddick 1 fauna, Marion County, Florida. Fossils of Desmodus from outside the Recent North American range of D. rotundus are known from late Pleistocene sites in northern Mexico, California, Arizona, New Mexico, Texas, Florida, West Virginia, and Cuba (Ray et al. 1988). Hutchison (1967) synonymized D. magnus with D. stocki on the basis of their similarity in size and other cranial features. Most recent workers have followed Hutchison in recognizing D. stocki as the only extinct late Pleistocene species in North America. Ray et al. (1988) mapped and briefly summarized all known fossil occurrences of vampire bats.

In Florida, *Desmodus stocki* has been recorded from four Rancholabrean vertebrate faunas (Ray et al. 1988). Most of these fossils were referred originally to *Desmodus* magnus. Over the past 20 years numerous early Pleistocene (Irvingtonian) vertebrate fossil sites have been discovered in peninsular Florida. Screenwashing for microvertebrates from these Irvingtonian localities has revealed the presence of a new species of *Desmodus* in three faunas: the early Irvingtonian Inglis 1A Local Fauna, Citrus County, and the middle Irvingtonian Haile 16A and Haile 21A local faunas, Alachua County. These fossils represent the oldest known vampire bats.

Meanwhile, in conjunction with field studies of bats and surveys of caves in Venezuela. Linares in 1965 recovered two geologically young fragmentary skeletons of a very large new species of vampire bat. Efforts by Linares and Ray to determine the affinities of this form led to comprehensive study of the fossil record of vampires and to comparison of the hard parts of the three living species. Our mutually overlapping and converging interests in fossil vampires have resulted in presentation of a synopsis of our findings (Ray et al. 1988) and in a more detailed review we have in progress. Delay in publication of that review has caused premature allusion in print to the new species from Florida and Venezuela. This, together with the intense current interest in vampires, has induced us to validate the names of the two new species without further delay.

The fossils utilized for this paper are deposited in the vertebrate paleontological collections of the Florida State Museum, University of Florida (UF) and the Florida Geological Survey (UF/FGS), also housed at the Florida State Museum; the Department of Paleobiology, U.S. National Museum of Natural History, Smithsonian Institution (USNM); Department of Vertebrate Paleontology, Los Angeles County Museum of Natural History (LACM); Sección de Paleobiología, Museo de Ciencias Naturales, Universidad Simón Bolivar, Caracas, Venezuela (MUSB). Recent comparative material is from the Division of Mammals, National Museum of Natural History, Smithsonian Institution (USNM), the Department of Mammalogy, American Museum of Natural History (AMNH), and the mammalogy collection of the Florida State Museum (UF). All measurements were taken with dial calipers and rounded to the nearest 0.1 mm. Descriptive morphological terms and cranial measurements follow DeBlase and Martin (1981).

Systematic Paleontology

Class Mammalia Linnaeus Order Chiroptera Blumenbach Family Desmodontidae Gill Genus Desmodus Maximilian Desmodus archaeodaptes, new species Fig. 1

D. praecursor. – Ray et al., 1988:20 (nomen nudum).

Desmodus archaeodaptes. – Ray et al., 1988: 22 et sqq. (nomen nudum).

Holotype.—UF 94526, nearly complete braincase posterior to interorbital constriction, lacking only zygomatic arches, with associated left periotic. Collected by Lawrence H. Martin, Jr., in May 1983.

Type locality.—Haile 21A Local Fauna of early Pleistocene (middle Irvingtonian) age, located 4.6 km northeast of Newberry, Alachua County, Florida.

Referred material. – UF 94527, UF 94528, two proximal ends of left humeri from type locality; UF 40046, complete right humerus, from Inglis 1A Local Fauna of early Pleistocene (early Irvingtonian) age, located 3 km southwest of Inglis, Citrus County, Florida; UF 24206, distal end of left humerus and UF 40047, proximal end of left radius, from Haile 16A Local Fauna of early Pleistocene (middle Irvingtonian) age, located 5.8 km northeast of Newberry, Alachua County, Florida.

Etymology.—From the Greek *archaios*, ancient, old, and *daptes*, eater of blood by

| Species and locality | Total length of skull | Condylobasal length | Breadth of rostrum | Interorbital constriction | Zygomatic breadth |
|---|---|--|---|--|---|
| Desmodus archaeodaptes (UF 94526, holotype) Haile 21A Florida | _ | - | - | 5.8 | 12.4 |
| <i>Desmodus rotundus murinus</i> Mexico | $\begin{array}{c} 23.7 \pm 0.44 \\ (22.7 - 24.3) \\ 30 \end{array}$ | $21.2 \pm 0.36 \\ (20.5-21.8) \\ 30$ | $\begin{array}{c} 6.0 \pm 0.21 \\ (5.56.5) \\ 30 \end{array}$ | $5.5 \pm 0.17 \\ (5.1-5.8) \\ 30$ | $\begin{array}{r} 12.0 \pm 0.29 \\ (11.5 - 12.7) \\ 30 \end{array}$ |
| Desmodus r. rotundus Chile and Paraguay | $\begin{array}{c} 24.8 \pm 0.53 \\ 24.1 25.5 \\ 10 \end{array}$ | $\begin{array}{c} 22.3 \pm 0.56 \\ (21.523.3) \\ 10 \end{array}$ | $\begin{array}{c} 6.6 \pm 0.28 \\ (6.17.0) \\ 10 \end{array}$ | $5.7 \pm 0.23 \\ (5.4-6.0) \\ 10$ | $\begin{array}{r} 12.8 \pm 0.28 \\ (12.3 - 13.1) \\ 10 \end{array}$ |
| <i>Desmodus stocki</i> San Josecito Cave Mexico | $27.3 \pm 0.52 \\ (26.5-28.2) \\ 6$ | $\begin{array}{c} 24.5 \pm 0.18 \\ (24.1 - 24.7) \\ 6 \end{array}$ | $7.4 \pm 0.16 \\ (7.1-7.6) \\ 6$ | $\begin{array}{c} 6.1 \pm 0.11 \\ (5.9 6.2) \\ 9 \end{array}$ | 14.0 ± 0 (14.0) 2 |
| <i>Desmodus stocki</i> Reddick Florida | _ | - | - | $\begin{array}{c} 6.1 \pm 0.21 \\ (5.8 6.3) \\ 3 \end{array}$ | $\begin{array}{c} 14.3 \pm 0.20 \\ (14.1 - 14.5) \\ 2 \end{array}$ |
| Desmodus draculae (MUSB 152-85 PB, holo- type; USNM 23568, paratype) Cueva del Guácharo, Venezuela | 31.2, — | 29.7, — | 9.2, — | 5.7, 6.7 | - |

Table 1.—Cranial and mandibular measurements of *Desmodus archaeodaptes*, *D. rotundus*, *D. stocki*, and *D. draculae*. Mean, standard deviation, observed range (in parentheses), and sample size are given for each measurement.

sucking. The name refers to the fact that this is the oldest known species of vampire bat.

Diagnosis. - Differs from other known species of Desmodus in possessing broad plate-like mastoid process, narrower occiput, lateral connection of nuchal crest to paroccipital process; and from all except D. draculae in nearly vertical orientation of supraoccipital, lack of inflation and ventral flexion of posterior portion of braincase, and posteriorly oriented foramen magnum with rounded dorsal margin. Desmodus archaeodaptes differs from D. rotundus in presence of larger glenoid fossa, reduced postglenoid process, smaller occipital protuberance, and weakly inflated supraoccipital; from D. stocki in smaller size, longer and narrower braincase, weaker cranial crests, ventrally deflected paroccipital process, shallow basicranial pits separated by low indistinct ridge, and weakly inflated posteromedial process of basisphenoid; and from *D. draculae* in much smaller size.

Measurements. - See Tables 1 and 2.

Description and comparisons. – The braincase of the holotype of Desmodus archaeodaptes from Haile 21A is nearly complete posterior to the interorbital constriction. The zygomatic arches are missing except for the base of the right squamosal process. This skull is within the size range of Recent D. rotundus and is considerably smaller than that of D. stocki and D. draculae (see Table 1 and Fig. 1).

Desmodus archaeodaptes more closely resembles D. rotundus than D. stocki in certain cranial features: these include narrower more elongated braincase, reduced cranial crests, ventral deflection of the paroccipital

Table 1.-Continued.

| Mastoid breadth | Breadth of braincase | Length of braincase | Height of braincase | Total length of mandible | Length of mandibu- lar tooth row | Height of coronoid |
|---|---|---|---|---|--|----------------------------------|
| 12.4 | 12.3 | 17.2 | 12.0 | - | - | - |
| $\begin{array}{c} 12.5 \pm 0.29 \\ (12.0 - 13.1) \\ 30 \end{array}$ | $\begin{array}{r} 11.9 \pm 0.24 \\ (11.5 - 12.5) \\ 30 \end{array}$ | $\begin{array}{c} 16.9 \pm 0.35 \\ (16.4 17.9) \\ 30 \end{array}$ | $ \begin{array}{r} 11.9 \pm 0.39 \\ (11.1-12.6) \\ 30 \end{array} $ | $\begin{array}{r} 15.3 \pm 0.33 \\ (14.5 - 16.0) \\ 30 \end{array}$ | $\begin{array}{c} 4.7 \pm 0.14 \\ (4.4 5.0) \\ 30 \end{array}$ | $6.1 \pm 0.20 \\ (5.6-6.5) \\ 3$ |
| $\begin{array}{c} 13.0 \pm 0.22 \\ (12.6 - 13.3) \\ 10 \end{array}$ | $\begin{array}{c} 12.6 \pm 0.32 \\ (12.1 - 13.0) \\ 10 \end{array}$ | $\begin{array}{c} 17.4 \pm 0.33 \\ (17.1 - 18.2) \\ 10 \end{array}$ | 12.3 ± 0.36 (11.9–12.6) 10 | $\begin{array}{c} 15.8 \pm 0.40 \\ (15.3 16.6) \\ 10 \end{array}$ | $\begin{array}{r} 4.8 \pm 0.09 \\ (4.7 - 4.9) \\ 10 \end{array}$ | 6.3 ± 0.26 (6.0–6.8) 10 |
| $\begin{array}{c} 14.1 \pm 0.33 \\ (13.5 - 14.5) \\ 8 \end{array}$ | $\begin{array}{c} 13.8 \pm 0.20 \\ (13.6 - 14.2) \\ 11 \end{array}$ | 19.2 ± 0.32 (18.7–19.7) 9 | $\begin{array}{c} 13.5 \pm 0.17 \\ (13.213.8) \\ 10 \end{array}$ | - | - | - |
| $\begin{array}{c} 14.4 \pm 0.25 \\ (14.1 - 14.7) \\ 5 \end{array}$ | $\begin{array}{c} 14.1 \pm 0.22 \\ (13.8 - 14.4) \\ 4 \end{array}$ | 19.6 ± 0.08 (19.5–19.7) 3 | 13.2 ± 0.19 (13.0–13.5) 4 | 17.4 ± 0.26 (17.0–17.6) 3 | $5.3 \pm 0.10 \\ (5.1-5.4) \\ 16$ | 6.7 ± 0.21 (6.2–6.9) 7 |
| 15.2, 15.5 | 14.8, 14.5 | 21.1, 22.4 | 14.8, 13.4 | 21.9, — | 8.5, 8.3 | 9.4, — |

process, weakly inflated posteromedial process of the basisphenoid, and shallow basicranial pits. There are also many characters that distinguish the skulls of D. archaeodaptes and D. rotundus. The occipital protuberance only slightly overhangs the occipital condyles in D. archaeodaptes, whereas in D. rotundus the braincase is expanded posteriorly and flexed ventrally so that the occipital protuberance occupies a more posteroventral position. The occipital protuberance is also larger in the living species and has a prominent posteriorly projecting process. In lateral view, the supraoccipital of *D. archaeodaptes* is nearly vertical, but in D. rotundus, because of inflation and ventral flexion of the braincase, it is tilted posteriorly. In the essentially unmodified braincase of D. archaeodaptes the foramen magnum faces posteriorly, whereas in D. rotundus it is oriented ventrally. The supraoccipital in D. archaeodaptes is essentially flat, but in D. rotundus the region along the midline between the foramen

magnum and the occipital protuberance is noticeably inflated. The occiput of D. archaeodaptes is narrower and higher than in the Recent species. The occipital protuberance is more dorsad, and the nuchal crests (forming the lateral borders of the occiput) make a more acute angle in D. archaeodaptes than in D. rotundus because they connect laterally to the paroccipital processes rather than to the mastoid processes. Laterally, the nuchal crest turns abruptly ventrad in D. archaeodaptes and becomes confluent with the lateral edge of the paroccipital process; a weak secondary crest branches from the lateral edge of the nuchal crest and connects with the mastoid process. In D. rotundus the mastoidal connection is emphasized and the paroccipital connection is lost.

The braincase of *Desmodus stocki* is larger overall and relatively shorter, broader, and more globose than that of *D. archaeodaptes* and *D. rotundus*, but is intermediate between these smaller species in certain oth-

| Species and locality | Total length | Proximal width | Distal width | Medial width of shaft | | |
|---|---|--|-----------------------------------|-----------------------------------|--|--|
| Desmodus archaeodaptes (UF 40046) | | | | | | |
| Inglis 1A Florida | 39.7 | 5.7 | 6.2 | 2.2 | | |
| (UF 24206) Haile 16A Florida | - | - | 5.9 | - | | |
| (UF 94527) Haile 21A Florida | - | 5.2 | - | 2.1 . | | |
| Desmodus rotundus | 37.0 ± 2.33 (32.4-42.4) 19 | $\begin{array}{c} 4.9 \pm 0.28 \\ (4.4 - 5.6) \\ 19 \end{array}$ | $5.4 \pm 0.30 \\ (4.8-5.9) \\ 19$ | $2.1 \pm 0.18 \\ (1.7-2.4) \\ 15$ | | |
| Desmodus stocki | | | | | | |
| San Josecito Cave Mexico (from Hutchison, 1967) | 43.6 (39.3–47.5) 42 | 6.3 (5.8–6.8) 47 | 6.8 (6.4–7.3) 52 | 2.5 (2.0–2.9) 56 | | |
| Reddick Florida | $\begin{array}{r} 41.8 \pm 1.34 \\ (39.4 - 44.3) \\ 15 \end{array}$ | $\begin{array}{c} 6.3 \pm 0.16 \\ (6.0 - 6.7) \\ 38 \end{array}$ | $6.8 \pm 0.18 (6.4-7.2) 42$ | $2.6 \pm 0.11 (2.2-2.7) 42$ | | |
| <i>Desmodus draculae</i> (MUSB 152-85 PB, holotype) Cueva del Guácharo Venezuela | 51.0 1 | - | 8.5 1 | 3.3 1 | | |

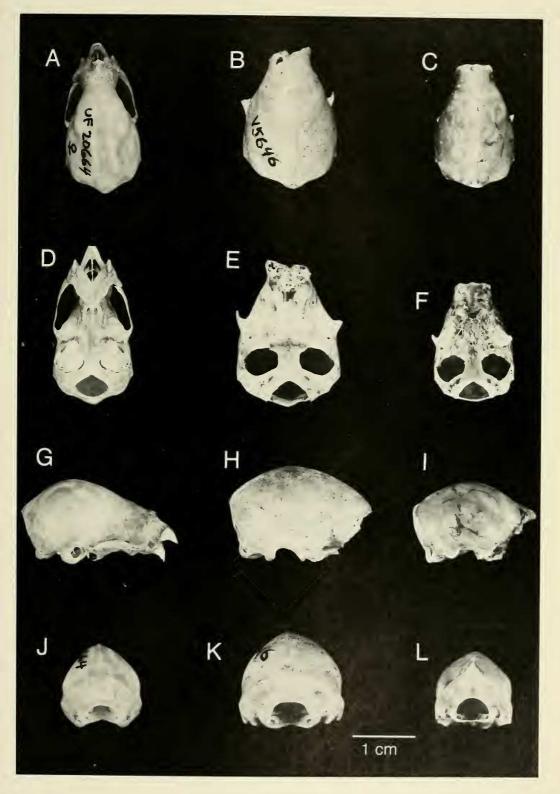
Table 2.—Measurements of the humerus of Recent and fossil *Desmodus*. Mean, standard deviation, observed range (in parentheses), and sample size are given for all measurements, except those taken from Hutchison (1967).

er characters. The posterior portion of the braincase of *D. stocki* is more inflated and the occipital protuberance and foramen magnum are located in a more ventral position than in *D. archaeodaptes*. Compared with *D. rotundus*, however, the braincase of *D. stocki* is not expanded as far posteriorly, nor does it attain the same degree of ventral flexion. The dorsal margin of the foramen magnum is rounded in *D. archaeodaptes* in contrast to its hexagonal shape in *D. stocki*. The cranium of *D. stocki* resembles that of the living species in the more ventral position of its occipital protuberance and the lateral connection of the nuchal crest to the mastoid process; these features give the occiput the appearance of being broader, but shallower, dorsoventrally than in *D. archaeodaptes.*

The articular surface of the glenoid fossa is relatively large in *Desmodus archaeodaptes* and *D. stocki*, and the postglenoid process is short and blunt. *Desmodus rotundus* has a smaller glenoid fossa and the postglenoid process is more elongated and triangular in shape. The smaller postglenoid

Fig. 1. Skulls of vampire bats in dorsal (A-C), ventral (D-F), right lateral (G-I), and posterior (J-L) aspect. A, D, G, J, *Desmodus rotundus*, UF 20664, Recent, Paraguay; B, E, H, K, *Desmodus stocki*, UF/FGS 5646, Rancholabrean, Reddick 1, Florida; C, F, I, L, *Desmodus archaeodaptes*, UF 94526 (holotype), Irvingtonian, Haile 21A, Florida. Scale is one cm.

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process of D. archaeodaptes and D. stocki, coupled with the larger articulating surface for the mandible, suggests that these extinct species may have had somewhat greater freedom of movement of the lower jaw than D. rotundus. The posteromedial process of the basisphenoid is weakly developed in the two smaller vampires, but is strongly inflated in D. stocki. The basicranial pits located anterior and medial to the tympanic cavity are barely noticeable depressions in D. archaeodaptes, but are larger, deeper, and extend farther posteriorly in D. stocki. In the larger species these pits are separated by a thin, knife-like ridge of bone that extends posteriorly to a point about halfway between the anterior and posterior edges of the tympanic cavity. This ridge is low and indistinct in D. archaeodaptes and disappears at the anterior edge of the tympanic cavity leaving the basioccipital almost perfectly flat. The basicranial pits and ridge are intermediate in their development in D. rotundus. The paroccipital process is ventrally deflected in D. archaeodaptes and D. rotundus, but oriented posteriorly in D. stocki. The broad ventrally rounded mastoid process of D. archaeodaptes is larger than that of D. stocki or D. rotundus.

The total length of the complete humerus from Inglis 1A referred to Desmodus archaeodaptes is within the observed range of humeri of Recent D. rotundus, although it is longer than any humerus measured of Middle American specimens referred to D. rotundus murinus (Table 2). The proximal and distal widths of this specimen slightly exceed those measurements in the same sample of D. rotundus. The length of the Inglis humerus barely overlaps the lower end of the range of variation of D. stocki humeri from Reddick 1C, while the proximal and distal widths are less than those for any humerus of D. stocki measured (Table 2). Two proximal ends of humeri from Haile 21A and a single distal end from Haile 16A are slightly smaller than the humerus from Inglis 1A, but are well within the observed range of measurements for Recent *D. rotundus.* There are no apparent characters, other than size, that differentiate the humeri of *D. rotundus, D. archaeodaptes,* and *D. stocki.*

Geologic age and localities. – Desmodus archaeodaptes is described on the basis of six specimens from three localities in northern peninsular Florida, all of which are early Pleistocene (Irvingtonian) in age. Biostratigraphic correlations with the North American Land Mammal biochronology establish Inglis 1A as very early Irvingtonian in age (between about 1.8 and 1.5 Ma), while Haile 16A and Haile 21A are middle Irvingtonian (between about 1.5 and 1.0 Ma). The oldest previously recorded vampire bats were samples of D. stocki from the late Pleistocene (early or middle Rancholabrean) Arredondo 2A and Reddick 1A, 1B, and 1C faunas, also from northern Florida. With the exception of the probably Recent remains from San Miguel Island, all fossils of D. stocki from the western United States and northern Mexico are latest Pleistocene (late Rancholabrean) in age (Kurten & Anderson 1980, Ray et al. 1988), a time interval during which Desmodus appears to have been absent from Florida (Morgan 1985).

Fossil sites representing former caves, fissures, and sinkholes are common in the karst terrain of northern peninsular Florida. Most of these sites are clastic infillings deposited in solution features developed in the soft marine limestones of the upper Eocene Ocala Group. These fossiliferous terrestrial sediments are most often exposed by commercial limestone mining. Many Florida State Museum vertebrate fossil sites are identified by numbers and letters following the general locality name (e.g., Haile 21A). The name (e.g., Haile) refers to the geographic location of the site, the number identifies the particular limestone quarry or specific area in which the site is (or was) located, and the letter refers to individual fossil deposits within one quarry or specific area. Even

though two or more fossil sites may be found in the same limestone quarry, it cannot be assumed without strong evidence that they are necessarily close in age or formed through similar depositional processes.

The Inglis 1A Local Fauna was collected from the north bank of the now-defunct Cross Florida Barge Canal in Citrus County, Florida, 3 km SW of Inglis (29°01'N, 82°42'W), SE ¼, SE ¼, Sec. 9, T17S, R16E, Yankeetown 7.5 minute quadrangle, U.S. Geological Survey (1955). The fossiliferous sediments, now completely excavated, consisted of alternating layers of sand and clay filling a large solution cavity in the Eocene Inglis Formation. The geology and stratigraphy of Inglis 1A were discussed by Klein (1971). A diverse chiropteran fauna occurs at Inglis 1A supporting geological evidence that this deposit represents a former cave. Comprehensive studies have been conducted on the birds (Carr 1980) and snakes and lizards (Meylan 1982) of this fauna, and a list of the mammals was given by Webb & Wilkins (1984). Inglis 1A contains mammals found in both late Blancan and early Irvingtonian faunas in Florida, including Glyptotherium cf. G. arizonae (Gillette & Ray 1981), Megalonyx leptostomus (Mc-Donald 1977), Trigonictis cf. T. macrodon (Ray et al. 1981), Chasmaporthetes ossifragus (Berta 1981), and Capromeryx arizonensis (Klein 1971), but lacks forms restricted to the Blancan, including Borophagus, Nannippus phlegon, and Equus (Dolichohippus). An early Irvingtonian age for this fauna is further indicated by the presence of Geomys propinetis (Wilkins, 1984) and Sigmodon curtisi (Martin 1979).

The Haile 16A Local Fauna was discovered in a limestone quarry 5.8 km NE of Newberry, Alachua County, Florida (29°41'N, 82°34'W), NE ¼, NE ¼, Sec. 25, T9S, R17E, Newberry 7.5 minute quadrangle, U.S. Geological Survey (1968). The fossil vertebrates at this site occurred in a large fissure with massive dark silty clays. The depth, areal extent, and stratigraphy of this deposit could not be determined accurately as it was destroyed by limestone quarrying operations before it could be excavated. Although all fossils from Haile 16A were obtained by screenwashing spoil piles, there is no evidence that the fauna is mixed. No list of the mammalian fauna from Haile 16A has been published; however, a few of the taxa have been studied, including Trigonictis (Ray et al. 1981), Geomys (Wilkins 1984), Erethizon (Frazier 1981), and Sigmodon (Martin 1979). According to Martin, Sigmodon libitinus, a species known only from Haile 16A, is intermediate between S. curtisi from the early Irvingtonian Inglis 1A fauna and S. bakeri from the late Irvingtonian Coleman 2A fauna. A middle Irvingtonian age for Haile 16A is also indicated by the presence of Megalonvx wheatleyi (McDonald 1977), Tapirus haysii, and an early species of *Pitymys*, and by the stage of evolution of Holmesina.

The Haile 21A Local Fauna is located 4.6 km northeast of Newberry, Alachua County, Florida (29°41'N, 82°33'W), SE 1/4, NE 1/4, Sec. 26, T9S, R17E, Newberry 7.5 minute quadrangle, U.S. Geological Survey (1968). This site was discovered in 1983 by Eric Kendrew and was worked by the Florida State Museum between October 1983 and March 1984. Fossils were initially recovered from Haile 21A after the land surface had been graded with heavy equipment in preparation for mining. The fossiliferous sediments consist of clays, sands, and limestone breccias filling a former cave or sinkhole roughly circular in outline, some 10 m in diameter and 5 to 7 m in depth. There are no previous published references to the Haile 21A vertebrate fauna. The fauna is overwhelmingly dominated by a large species of *Platygonus*, similar to samples of Platygonus from other Irvingtonian sites in Florida. The occurrence of Smilodon gracilis suggests a pre-late Irvingtonian age for Haile 21A (Berta 1987), and the presence of Tapirus haysii and the association of Canis edwardii and C. armbrusteri are in-

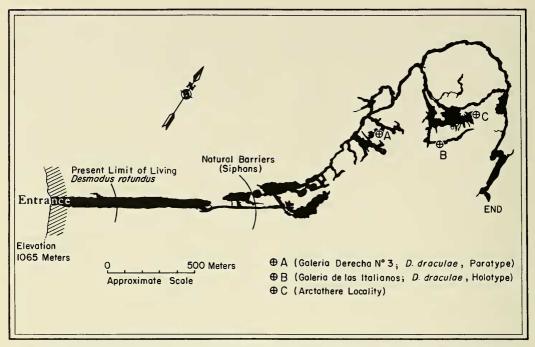


Fig. 2. Sketch map of Cueva del Guácharo, Monagas, Venezuela, the type locality of *Desmodus draculae*. In part after Anonymous, 1968, with modifications and additions by Linares.

dicative of Florida middle Irvingtonian faunas.

Desmodus draculae, new species Fig. 2-8

- "Una forma de *Desmodus* posiblemente del Pleistoceno . . . mayor que todas las conocidas . . . una nueva especie."—Linares 1968:138–139.
- "A new species of *Desmodus* from Venezuela."-Martin 1972:326.
- "A new species of fossil vampire bat from Venezuela."-Wołoszyn & Mayo 1974: 260.
- Desmodus sp.-Smith, 1976:66.
- "Fossil *Desmodus* larger than all previously known forms."—Greenhall et al. 1983:1.
- Desmodus draculae. Linares, 1987:11 (figured on p. 10). – Ray et al., 1988:20 et sqq., figs. 2–5 (nomen nudum).

Holotype. – MUSB 152-85 PB, skull, mandible, skeletal parts. Skull lacks zygo-

matic arches and all teeth save incisors; mandible essentially complete, retains right canine and all postcanine teeth and left P_4 ; skeletal parts include left humerus, distal two-thirds (with ulnar sesamoid in place) and head of right humerus, distal half or more of left and right radii, with vestiges of coossified ulnae, and three vertebrae. All elements white in color, thoroughly leached and chalky in texture though retaining sharp surface detail, except for the radii, which are in part deeply pitted. Collected by Omar J. Linares, 10–18 Apr 1965.

Type locality. – Cueva del Guácharo, District of Caripe, State of Monagas, Venezuela (Fig. 2), $10^{\circ}10'27''$ N, $62^{\circ}33'07''$ W. This cave has been described, illustrated, and mapped by the Sociedad Venezolana de Espelcología in its Boletín (Anonymous 1968, 1971). The cave is at least 9425 meters long, of which the first 1041 meters (known as the Tourist Zone) is the more readily accessible, and is terminated by nat-

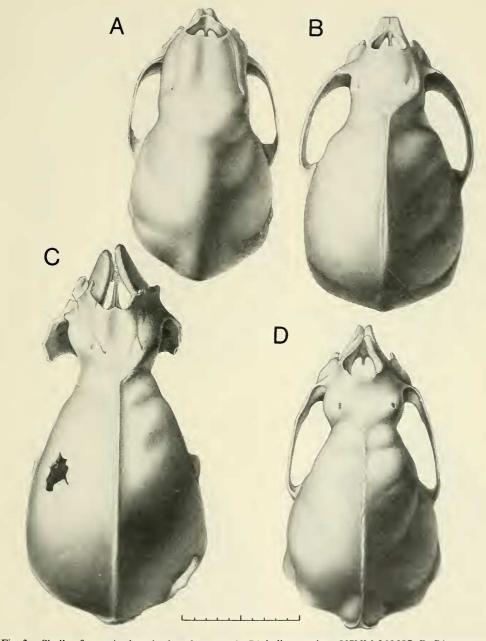
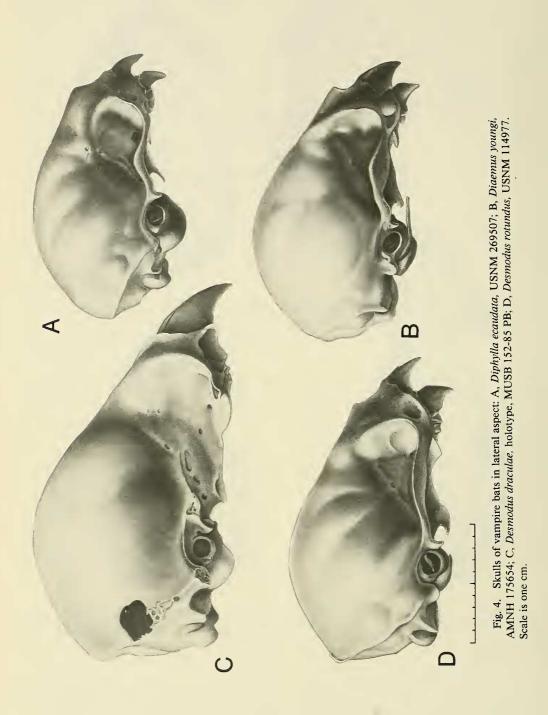


Fig. 3. Skulls of vampire bats in dorsal aspect: A, *Diphylla ecaudata*, USNM 269507: B, *Diaemus youngi*, AMNH 175654; C, *Desmodus draculae*, holotype, MUSB 152-85; D, *Desmodus rotundus*, USNM 114977. Scale is one cm.

ural barriers in the form of siphons. The type specimen of *D. draculae* was collected at the surface on the floor of the Galería de los Italianos, locality B on our sketch map (Fig. 2), at least 1973 meters from the present entrance of the cave, and some 1400 meters beyond the limit of living *D. rotundus.*



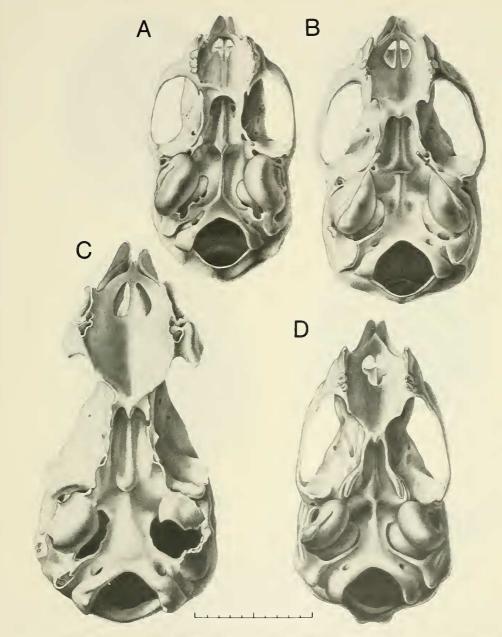


Fig. 5. Skulls of vampire bats in ventral aspect: A, *Diphylla ecaudata*, USNM 269507; B, *Diaemus youngi*, AMNH 175654. C, *Desmodus draculae*, holotype, MUSB 152-85 PB; D, *Desmodus rotundus*, USNM 114977. Scale is one cm.

Paratype.—USNM 23568, incomplete skull, lacking most of facial region and all teeth; incomplete mandible lacking posterior ends of rami and all teeth except base

of right canine; postcranial fragments, including fragment of right scapula, and fragments of left and right humeri, radii (with coossified portions of ulnae), and femora.

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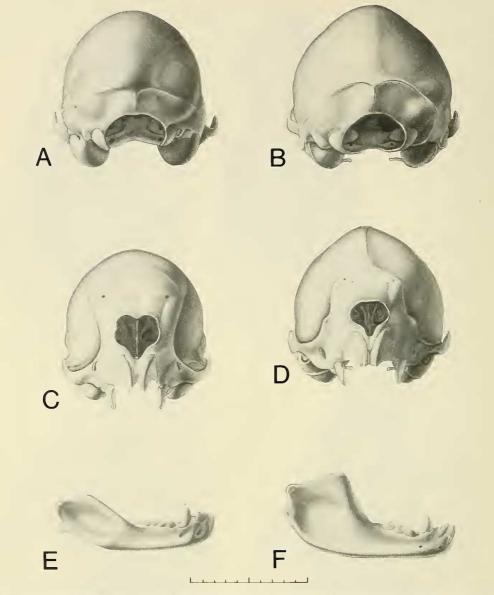


Fig. 6. Skulls and jaws of vampire bats. Skulls in posterior aspect: A, *Diphylla ecaudata*, USNM 269507; B, *Diaemus youngi*, AMNH 175654. Skulls in anterior aspect: C, *Diphylla ecaudata*, USNM 269507; D, *Diaemus youngi*, AMNH 175654. Right mandibular rami in labial aspect; E, *Diphylla ecaudata*, USNM 269507; F, *Diaemus youngi*, AMNH 175654. Scale is one cm.

Preservation similar to that of holotype, but not as good. Two proximal ends of right radii indicate still another individual. Collected by Omar J. Linares, 10–18 Apr 1965, at locality A, Cueva del Guácharo (Fig. 2).

Etymology.—The specific epithet of this largest known chiropteran vampire com-

memorates Count Dracula, the greatest human vampire of folklore (Wolf 1975).

Diagnosis. — A Desmodus larger than any other known form (greatest length of skull more than 31 mm vs. 27.4 maximum for D. stocki, length of humerus 51 mm vs. 47.5 maximum for D. stocki), but skull more

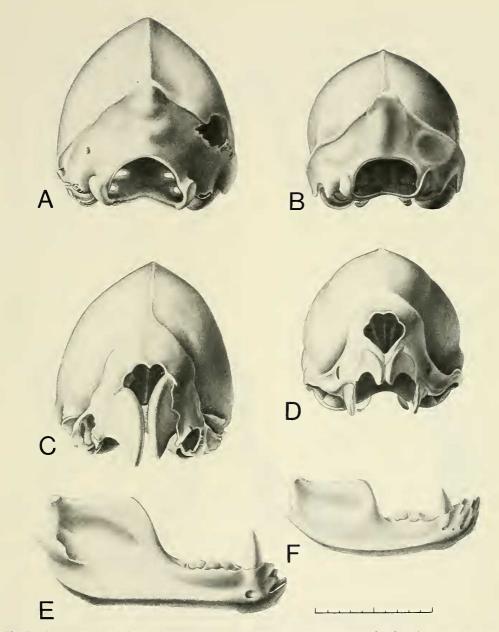


Fig. 7. Skulls and jaws of vampire bats. Skulls in posterior aspect: A, *Desmodus draculae*, holotype, MUSB 152-85 PB; B, *Desmodus rotundus*, USNM 114977. Skulls in anterior aspect: C, *Desmodus draculae*, holotype, MUSB 152-85 PB; D, *Desmodus rotundus*, USNM 114977. Right mandibular rami in labial aspect: E, *Desmodus draculae*, holotype, MUSB 152-85 PB; F, *Desmodus rotundus*, USNM 114977. Scale is one cm.

slender and delicate. Mandible with ventral border straight in lateral aspect and with pockets behind incisors virtually nonexistent.

Description and comparisons. – Except as otherwise indicated here, characters of skull of Desmodus draculae essentially as in D. rotundus. Skull long and narrow; facial region even more reduced; interorbital con-

Measurements. - See Tables 1 and 2.

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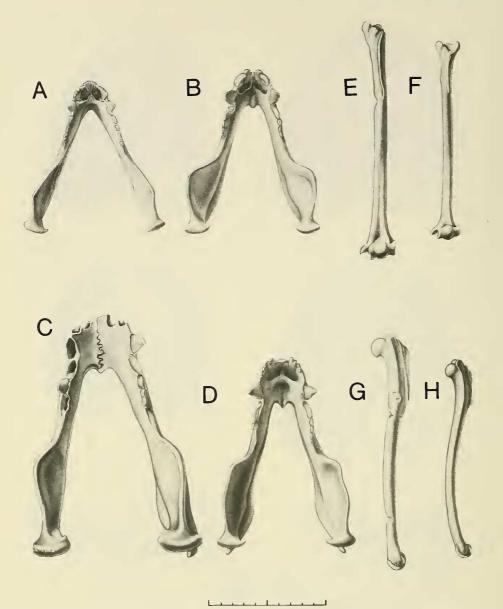


Fig. 8. Jaws and humeri of vampire bats. Mandibles in dorsal aspect: A, *Diphylla ecaudata*, USNM 269507; B, *Diaemus youngi*, AMNH 175654; C, *Desmodus draculae*, holotype, MUSB 152-85 PB; D, *Desmodus rotundus*, USNM 114977. Left humeri in cranial aspect: E, *Desmodus draculae*, holotype, MUSB 152-85 PB; F, *Desmodus rotundus*, USNM 114977. Left humeri in medial aspect; G, *Desmodus draculae*, holotype, MUSB 152-85 PB; H, *Desmodus rotundus*, USNM 114977. Scale is one cm, pertaining to A–D. Length of E and G is 51 mm, and F and H, 42.1 mm.

striction even farther forward and relatively greater; zygomatic ramus of maxilla directed more posteriad; occipital margin less clearly lyriform, with only suggestion of median lambdoidal extension; nasals even more reduced and depressed; maxillae scarcely expanded lateral to nasals. In lateral aspect, rostrum even more upturned and nares even more dorsally directed than in *D. rotundus*; dorsal profile of skull slopes forward from high braincase on a smooth line, uninterrupted by the slight nasal projection seen in *D. rotundus*. In ventral aspect, bullae are seen to be still more reduced than in *D. rotundus*, and are firmly coossified with skull anteriorly and posteriorly (as seen posteriorly in *Diphylla ecaudata*); palate longer and narrower, incisive foramina smaller than in *D. rotundus*.

Mandible also as in *D. rotundus* except as indicated here. Pockets behind incisors for reception of tips of upper incisors hardly discernible. Tips of upper incisors apparently would have rested medial to inner lower incisors, not in part behind them. In lateral aspect, ventral border of mandible quite straight, not curved as in *D. rotundus*; posteriorly it curves abruptly dorsad toward angular process. Posterior part of mandible overall resembles that of *Diaemus youngi* rather than *Desmodus rotundus*.

The postcranial parts preserved exhibit few distinctions from Desmodus rotundus and D. stocki other than larger size and concomitant robustness. The entepicondylar process of the humerus is more slender in proximodistal expansion than is that of D. rotundus and D. stocki. Although all specimens of the radius and ulna are incomplete, deeply pitted, and poorly preserved, it does appear that the shaft of the ulna distal to its coossification with the radius is more reduced than in D. rotundus and D. stocki. In none of the specimens can the ulnar shaft be traced with certainty far beyond the point of fusion; additional, better-preserved specimens will be needed to resolve the point.

A few fragments each from cave deposits in Yucatán and West Virginia represent large vampires of uncertain affinities, but possibly related to *D. draculae* (Ray et al. 1988).

Geologic age. – Quaternary. Unfortunately there is little basis on which to suggest an age for this material. The remoteness of the site within the cave, the occurrence of an arctothere in the same sector (Fig. 2, locality C), and the presumed extinct status of the species, all suggest an early, possibly late Pleistocene, age. The rotten condition of the bones and occurrence at the surface in a wet, active cave, in the same sector with similarly preserved remains of *Desmodus rotundus* and *Diphylla ecaudata*, are more consistent with a late, possibly Recent age. Only additional discoveries of fossils in a more revealing geologic context, or of living *D. draculae*, will resolve the problem.

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(GSM) Department of Natural Sciences, Florida State Museum, University of Florida, Gainesville, Florida 32611; (OJL) Departamento de Estudios Ambientales, Division de Ciencias Biologicas, Universidad Simón Bolivar, Caracas, Venezuela; (CER) Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.